

SEASONAL OCCURRENCE AND MATING AT FLOWERS BY
ANCISTROCERUS ANTILOPE
(HYMENOPTERA: EUMENIDAE)

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Abstract.—The eumenid *Ancistrocerus antilope* (Panzer) is scarce at flowers in early summer, but abundant by late summer. Samples systematically collected at flowers are strongly male biased while comparable samples reared from trap nests are female biased. This indicates that males spend a greater proportion of their time at flowers than do females. Females visit flowers for nectar, but the males also search flowers for mates. Mating is initiated at flowers, but may be completed elsewhere.

Eumenid wasps, like many other insects, seek mates at blossoms, nest sites and other resources (Parker, 1978). The site or sites chosen and the details of the search strategy differ among species. Males of the colonial soil-nester *Euodynerus crypticus* (Say) wait on vegetation overlooking the colony and pounce on passing females (Vest, 1936) or visit nest entrances, paying particular attention to those that contain advanced females (Isley, 1913). The non-colonial *Paraleptomenes miniatus* (Saussure) builds two-celled mud nests in sheltered areas, one cell containing a male and the other a female. The male emerges first, remaining on the nest to mate with his sister who emerges a little later (Jayakar and Spurway, 1966). *Euodynerus foraminatus* (Saussure) and *Ancistrocerus adiabatatus* (Saussure) nest in vacant insect tunnels in dead wood and exhibit comparable sibling mating. Females not inseminated as they emerge from their natal nest mate later on flowers or foliage (Cowan, 1979, 1981). *Epsilon* sp. has a similar mating system (Smith and Alcock, 1980).

In contrast to the species that copulate at nest sites, males of other eumenids seek mates where females gather water or mud for nest construction. Smith and Alcock (1980) reported mating at pools on an ephemeral stream by *Abispa ephippium* (Fabricius), and at small farm ponds by two species of *Paralastor*. Iwata (1953) observed copulation by several species of *Eumenes* along the edge of a brook.

Although many species of Eumenidae are common and important components of the insect community at flowers, their activities at these sites have not been the subject of careful study. We here present data indicating that for at least one eumenid, *Ancistrocerus antilope* (Panzer), flowers are apparently the primary site for encounters between the sexes.

Females of *A. antilope* nest in tubular cavities in wood. The female deposits an egg in the cavity and then brings in enough paralyzed caterpillars for the complete growth of one offspring. She then seals the cell with a mud partition. Oviposition, provisioning, and partitioning are then repeated until the cavity is filled with a linear series of cells. Females are opportunistic and readily accept artificial nest sites (trap-nests) consisting of wooden blocks with drilled holes (Cooper, 1953; Krombein, 1967).

MATERIALS AND METHODS

This study is based on observations of the sex ratios and mating behavior of *A. antilope* adults reared from trap nests or collected at blossoms. Unless otherwise indicated, the observations were made on or near the University of Michigan Biological Station (UMBS) in Emmet and Cheboyan cos., Michigan in 1982. The sex ratio at blossoms was estimated from samples taken with an aerial net for three hours in late morning about once a week from June 8 to September 4 along a transect that followed Reed Rd. in Emmet Co. (Waldbauer, 1983). The sex ratio of the whole population was estimated from a sample reared from trap nests. Seventy-five bundles of five trap nests each were placed on UMBS property; all were within three to five miles of the Reed Rd. transect. Each trap nest was a 19 mm × 19 mm × 150 mm block of pine with a drilled hole about 135 mm deep. Each bundle of five had one nest each with hole diameters of 4.8, 5.6, 6.4, 7.1 and 7.9 mm. Occupied nests were taken into the laboratory, opened and the larvae reared to adulthood in individual chambers made from depressions in wooden blocks covered with microscope slides. Behavior was observed at flowers in Emmet Co. in 1982 and 1983 and at trap nests from which adults were emerging in the field from 1976 to 1980 (Cowan 1979, 1981) in Washtenaw and Kalamazoo Cos., Michigan.

The data were analyzed by means of a chi square test of independence using a 2 × 2 contingency table. Yates' correction for continuity was applied.

RESULTS

Ancistrocerus antilope was scarce at blossoms in June and early July, but was abundant from late July through August (Table 1). The individuals caught in June, and perhaps those taken in early July, presumably represent the diapausing population that overwintered as prepupae from the previous summer. The individuals caught from July 28 onward presumably represent the summer generation, whose offspring will enter diapause and lie dormant until the following June. The blossoms visited and the number of *A. antilope* taken at each are as follows: *Anemone canadensis* L. (Ranunculaceae), 1; *Cornus stolonifera* Mich. (Cornaceae), 2; *Pastinaca sativa* L. (Umbelliferae), 85; *Solidago* spp. (*S. rugosa* Mill., *S. canadensis* L. and *S. gigantea* Ait.) (Compositae), 108; *Viburnum trilobum* Marsh. (Caprifoliaceae), 1; other blossoms, 4. The great majority was, of course, taken at *P. sativa* and *Solidago* spp., plants that blossom from mid- to late summer. The preference for *Solidago* spp. is marked, and may have been even more striking before *Pastinaca sativa* was introduced from Europe.

The observations made at nests from which young adults were emerging indicate that males of *A. antilope* do not frequent nesting areas in search of mates. The wasps simply emerge and disperse. Males were never seen lingering or returning

Table 1. The seasonal occurrence of *Ancistrocerus antilope* adults at blossoms in 1982 along the Reed Rd. transect in Emmet Co., Michigan.

	June				July				August				September	Total
	8	14	23	30	6	13	20	28	6	12	18	25	4	
No. males	0	0	0	1	0	0	2	22	48	57	14	26	8	178
No. females	2	1	0	0	0	1	0	0	3	0	0	2	0	9

to the nest area, as is the case with other eumenid species (Cowan, 1979, 1981; Smith and Alcock, 1980).

The behavior of male and female *A. antilope* visiting blossoms differed markedly. Females flew comparatively slowly and directly from one inflorescence to another. When they landed, they spent a few tens of seconds feeding before departing. Males, although they also fed at flowers, were much more often seen flying quickly from flower to flower, where they hovered or circled briefly before moving on. If a eumenid was on the flower, males of *A. antilope* dropped down to touch it lightly, but quickly moved on if it was not a female *A. antilope*. Males patrolling flowers sometimes encountered one another and briefly hovered or circled before going their separate ways.

The sample of *A. antilope* that emerged from trap nests during mid- to late summer of 1982 indicates that the non-diapausing generation was strongly female biased (22 males and 35 females). However, the following diapausing generation (progeny of the 1982 summer generation) was found to be male biased, as indicated by the emergence of a total of 16 males and 4 females from overwintered trap nests in spring of 1983. These sex ratios are significantly different ($\chi^2 = 9.98$, 1 df, $P < 0.005$). More extensive unpublished data from Kalamazoo Co., MI, also indicate a male bias in the diapausing generation. Similar male biases have been observed by other workers (Fye, 1965; Longair, 1981) and are to be expected on theoretical grounds (Seeger 1983). The sample of *A. antilope* collected at blossoms was extremely male biased (178 males and 9 females) and differs significantly from the sample of non-diapausing wasps (22 males and 35 females) reared from trap nests ($\chi^2 = 90.6$, $P < 0.0005$).

On three occasions in early August of 1982 or 1983 we collected coupled male and female *A. antilope* at blossoms. Two pairs were associated with either *Solidago* sp. or *Pastinaca sativa*, but no host plant record was kept. The third pair was caught on an inflorescence of *Solidago* sp. In a fourth instance we observed the initiation of pairing. A female feeding on a *Solidago* inflorescence was discovered by a male. He immediately landed on her and began courtship. Within a few seconds, a second male discovered the pair and landed on top of the first male. A struggle ensued; the trio fell to the ground and the second male was dislodged. Then the coupled pair flew up into nearby trees.

DISCUSSION

Despite diligent observation, we have not seen interactions between the sexes at *A. antilope* nests, either while the females were provisioning them or later when newly molted adults were emerging. If mating does occur at the nests, it is rare. Mating, therefore, can be expected to occur at some resource for the females such

as nectar flowers or mud and water for building nest partitions. We have not made observations at the sources of building material, nor can we eliminate the possibility that mating occurs at a mating area (lek) that is not associated with a resource. Our observations do indicate that flowers are an important, if not the sole, mating site for *A. antilope*.

Our contention is supported by: 1) the discovery of several mating pairs on nectar blossoms, 2) the observation that males, unlike females, patrol inflorescences in an apparent search for mates, and 3) the extreme difference in sex ratio between samples taken at flowers and samples that emerged from trap nests. This difference in sex ratios apparently results from the different activities of the sexes. Females devote most of their time to nesting activities which keep them scattered in wooded areas where nest sites and prey occur. Only occasionally do they visit flowers to obtain nectar. (In forested areas patches of suitable flowers may be localized.) The males, on the other hand, presumably devote their time almost exclusively to searching for mates. Thus, they predominate in samples from flowers because, in addition to feeding, they remain at the flowers in search of females.

Although male and female *A. antilope* often meet on inflorescences, they apparently finish mating elsewhere. In the laboratory a pair may stay together for over 80 minutes and may copulate several times before separating (Cowan, unpublished; Cooper, 1955). Thus, the relative paucity of mating pairs at blossoms suggests that pairs leave the blossoms to finish mating. They may fly some distance away, as did the one pair that we watched; perhaps some hide below the foliage of the nectar plants. At any rate, it seems that they seek out a hiding place where they will not be conspicuous to predators or interloping males.

The eumenids *A. adiabatus* and *E. foraminatus* are found in the same habitats and have nesting behavior similar to *A. antilope*, but the first two species mate at emergence sites. This difference may be at least partly explained by the fact that female *A. adiabatus* and *E. foraminatus* mate with only one male (Cowan, 1981), while female *A. antilope* mate with more than one male (Cowan, unpublished). If, as is typical with other insects (Parker, 1970), the last male to mate with a female before oviposition fertilizes the majority of her eggs, then there would be little reward to a male *A. antilope* for being the first to locate a female. The eumenid with a known mating system most similar to that of *A. antilope* is *Abispa ephippium* (Smith and Alcock, 1980). In this species, males patrol stream banks rather than flowers; the paired wasps fly together into foliage where they copulate repeatedly before separating. The females are also receptive to more than one male.

Alcock et al. (1978) identified two key factors determining male reproductive behavior of wasps and bees: 1) whether females mate only once or multiply, 2) the distribution of receptive females. Although we have some information for a few species of Eumenidae, the ultimate reasons for single or multiple mating by females and the ecological determinants of individual distribution in nature remain obscure.

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